

FLORISTICS AND DISTRIBUTION OF VERNAL POOLS ON
THE COLUMBIA PLATEAU OF EASTERN WASHINGTON

CURTIS R. BJÖRK

Stillinger Herbarium, University of Idaho, Moscow, ID 83843
e-mail: cbjork@onewest.net

PETER W. DUNWIDDIE

The Nature Conservancy of Washington,
217 Pine St., Ste. 1100, Seattle, WA 98105
e-mail: pdunwiddie@tnc.org

ABSTRACT. Vernal pools are common on the Columbia Plateau of eastern Washington, where they occur on basalt bedrock within the channels scoured by the Pleistocene Missoula Floods. This is the first extensive floristic survey of these pools. Eighty-five percent of the 283 plant taxa are native, and the majority of these are annual. The Washington vernal pools have strong floristic affinities with their counterparts in California; 34% of the native species and 65% of genera in the Columbia Plateau pools also occur in California vernal pools. The remainder include numerous regional and locally endemic taxa. The total native flora is two-thirds that of the California vernal pools, but the average per-pool taxon richness in Washington is greater.

Key Words: vernal pools, Columbia Plateau, Washington, floristics

Vernal pools have long been recognized for their rich and unique biota (Jain and Moyle 1984; Purer 1939; Witham et al. 1998; Zedler 1987). These closed-basin non-wooded habitats containing standing water accumulated from precipitation during the cool season and fully desiccated in summer. They have been well documented within the California Floristic Province, which encompasses the area from southwestern Oregon to Baja California del Norte and inland to the Sierra Nevada (Hickman 1993). However, their existence elsewhere in western North America has been largely overlooked. A large number of seasonal and permanent wetlands occur in the Columbia Plateau of eastern Washington (Figure 1). Many of these wetlands are vernal pools that share abiotic features as well as plant and animal taxa with their Californian counterparts.

There are no published floristic surveys of the vernal pools in eastern Washington. One ecological study examined the relationships between soil and plant distributions around a set of pools in Adams County (Crowe et al. 1994) and another examined the ecology of non-native plants in the same set of pools (Brown 2001). Our investigation was

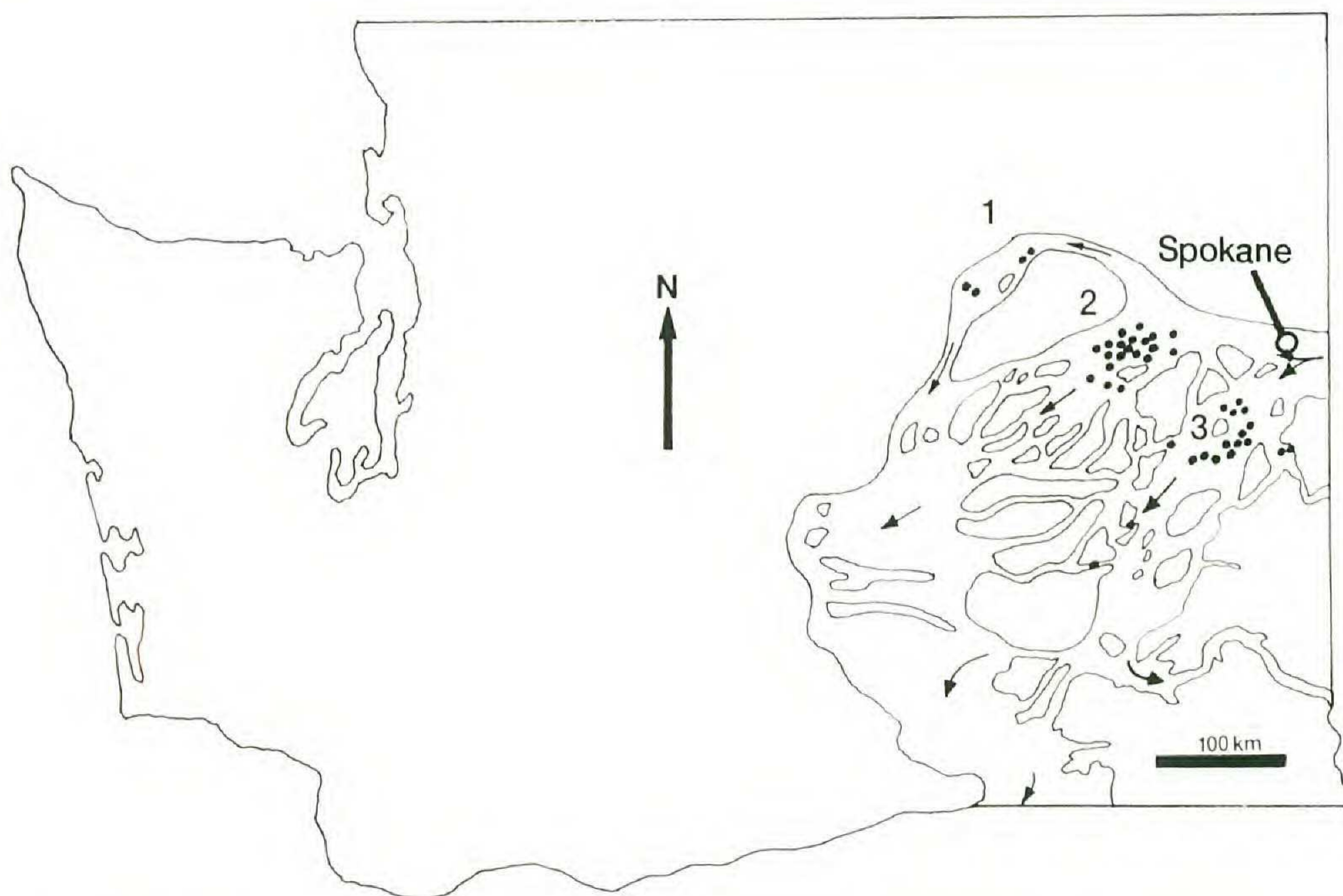


Figure 1. Map of Washington State, showing channels of the Missoula Flood events and study sites. Arrows indicate direction of water flow during floods. Polygons within the flood area indicate upland sites of loess soil that escaped the scouring of the floods. Dots indicate locations of vernal pools and vernal pool complexes studied. Numbers refer to the three main groupings of flood channels on the Columbia Plateau.

initiated to provide basic floristic information on this little-studied region. Specifically, we sought to: (1) determine the geographical extent of vernal pools in the Columbia Plateau of Washington, (2) generate lists of vascular plants associated with the pools, (3) compare their floristic composition with the vernal pools of California, (4) identify taxa that distinguish the Columbia Plateau vernal pools from those of other vernal pool regions, and (5) bring the high ecological value of these vernal pools to the attention of the public and scientific community.

Study area. The Columbia Plateau is a landscape of Miocene flood-basalts overlain by loess, sand, and gravel. A series of immense Late Glacial flood events, known as the Missoula Floods (ca. 15,000 to 12,000 YBP) scoured away loess hills in broad channels, leaving bedrock exposed in a region referred to as the Channeled Scablands (Bretz 1969). There are three main groupings of Missoula Flood channels (Figure 1). The westernmost occur in and around the Grand Coulee; a central group occurs in central Lincoln and Adams Counties; and the eastern channels extend from near Spokane southwestward into southeast Lincoln and

eastern Adams Counties. These channels contain a major concentration of wetlands that occur in shallow basins perched on the basalt bedrock, which is effectively impervious to groundwater movement. Surface drainage is limited to small creeks and intermittent streams.

Precipitation on the plateau is of a Mediterranean pattern, with a winter maximum/summer minimum. Evapotranspiration differs greatly between the cold, humid winters and the hot, arid, nearly cloudless summers. Total precipitation ranges from an average of 23 cm at Coulee City in the west to 36 cm at Spokane in the east (United States Department of Commerce 1973). In the first year of our study, winter precipitation (November–April, 1996–97) averaged 42% above normal, with below-normal temperatures. The second year was significantly warmer and drier, with winter precipitation averaging only 83% of normal across the study area. Water levels and duration of flooding in the pools contrasted greatly between the two years.

MATERIALS AND METHODS

Satellite photographs and ground searches were the primary means used to identify seasonal wetlands in the Scablands. We distinguished California-type vernal pools from other seasonal basin wetlands in the study area based on three criteria: (1) annuals dominant and woody component minimal, (2) lack of surface salt deposits, and (3) presence of taxa characteristic of vernal pools in California, including *Plagiobothrys* sect. *Allocarya*, *Psilocarphus* spp., and *Navarretia leucocephala* subsp. As an additional aid in finding study sites, we sought location information from herbarium specimens of characteristic vernal pool taxa in regional herbaria at Washington State University, Pullman and University of Washington, Seattle (ws and wtU, respectively). However, there were very few collections of these plants from the Columbia Plateau, and most lacked precise location information.

All vascular plant taxa were recorded for 242 vernal pools from April–July, 1997 in Spokane, Adams, Lincoln, Grant, and Okanogan Counties. In 1998, a total of 110 more pools were surveyed, mostly in the Swanson Lakes Wildlife Management Area. We visually estimated pool area and depth. Taxa were recorded as present within vernal pools if we observed them at or below the obvious high-water mark of the current season. Voucher specimens of taxonomically questionable or rare taxa were deposited in wtU and ws. Nomenclature is mostly from Hickman (1993) and generic placement is largely based on APG classification (Angiosperm Phylogeny Group 1998).

Water levels were extremely high in 1997, resulting in the inundation of some adjacent uplands that contain dryland taxa not normally found in vernal pools. Subsequent death of large sagebrush in some of these flooded areas confirmed that water levels had been abnormally high. This inundation frequently resulted in mixing of amphibious vernal pool taxa with those of the surrounding upland communities. Since we sought to characterize the flora typical of pools during normal seasonal inundation, we identified a "core flora" that excluded taxa not well suited to the vernal pool environment. The excluded taxa are not persistent and are unable to withstand the flood or drought stage of vernal pool hydrology.

RESULTS

Vernal pool habitats. California-type vernal pools occur in Adams, Douglas, Grant, Lincoln, Okanogan, and Spokane Counties, where they are all limited to the flat, impervious basalt bedrock exposed by the Missoula Floods. The pools are concentrated in three distinct regions delineated by the Missoula Flood channels. The greatest concentration occurs in the central channel, in and around the Swanson Lakes Wildlife Management Area, which includes some of the least disturbed lands in the Scablands. Vernal pool densities exceed 200 per square-mile section (2.6 km²) in some areas. The flood channels are separated from each other by expanses of hilly loess uplands averaging approximately 20–30 km wide. No vernal pools occur on these intervening loess hills.

The vernal pools examined in Washington were typically small and shallow. They ranged in area from 3–4608 m² with an average of 1592 m². Mean minimum depth was 0.47 m. Pools in the eastern channels were smaller (mean and SE = 123 ± 59 m²) than pools in the west (635 ± 169 m²; $p = 0.04$) and central channels (2263 ± 488 m²).

Most of the Columbia Plateau vernal pools lie within a shrub-steppe mosaic composed of sagebrush (*Artemisia* spp.) and various codominant grasses and forbs. In northern and eastern portions of the plateau, they are scattered in open *Pinus ponderosa* stands. Pools in the central and western flood channels are mostly surrounded by shrub-steppe/grassland mosaic. Although many sites are only moderately disturbed, with minimal cover of non-natives, perhaps half of the pools are surrounded by communities significantly altered by non-native taxa such as *Apera interrupta*, *Bromus* sect. *Eubromus*, *Hypericum perforatum*, *Lactuca serriola*, *Poa bulbosa*, *Sisymbrium altissimum*, and *Taeniatherum caput-medusae*.

In 1997, most vernal pools began to dry at the end of May, though very large pools retained standing water through June. In contrast, in

1998, nearly all vernal pools were fully desiccated by the middle of April. We found that small pools were the first to fill with the onset of autumn rains, which occurred in late November in 1997. Large pools did not fill until midwinter, when rainwater and snow melt accumulated during warm Pacific storms. Even in the 1998 drought, medium and large pools held standing water continuously from first flooding until mid-April.

Soils of the vernal pools are grayish silty clays formed in part from volcanic ash. Nitrogen fixation in inorganic vernal pool soils may be primarily from abundant *Nostoc* colonies. Other sources of fixed nitrogen (i.e., Cyanolichens and legumes) are not abundant in vernal pool basins on the Columbia Plateau. Organic matter is minimal, but we observed significant accumulations of organic matter in some east-channel pools where mosses and thatch-forming taxa such as *Carex athrostachya* and *Senecio hydrophiloides* were more abundant.

Most vernal pools form on large expanses of exposed clay with little surface cover. This is particularly apparent post-desiccation, after plant senescence. Cobble-sized basalt rocks are common in many basins, sometimes providing complete cover throughout. Algal mats sometimes form dense cover, typically around *Eleocharis macrostachya* stands and in pools adjacent to roadways. Litter cover is typically minimal, except on margins, among *E. macrostachya* and in pools having abundant thatch-forming non-natives like *Bromus hordaceus*, *Cirsium arvense*, *Elytrigia repens*, *Lactuca serriola*, and *Taeniatherum caput-medusae*.

Moss cover is typically limited to marginal areas, where *Bryum algovicum*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Physcomitrium kellermanii*, *P. pygmaeum*, *P. pyriforme*, and *Tortula bistratosa* sometimes form a distinct band. In the eastern Missoula Flood channel, *Cratoneuron commutatum* and *C. filicinum* sometimes provide dense cover across pool basins. *Orthotrichum rivulorum* is locally common on basalt cobbles in the eastern channel. Liverwort diversity is limited to pool margins, where blooms of *Riccia beyrichiana*, *R. cavernosa*, *Ricciocarpos natans*, *Fossombronia* sp., *Sphaerocarpos mitchellii*, and *S. texanus* form. Of lichens, *Dermatocarpon meiophyllizum*, *D. minutum*, *Leptogium californicum*, *L. lichenoides*, *L. subaridum*, and *Aspicillia* aff. *contorta* are the only common taxa known to us in pool basins, where they grow on cobbles.

All vernal pools we surveyed are bordered by or are in the near vicinity of Mima mounds, which on the Columbia Plateau are round knolls of loamy soil about 1 m high, often perched on bare basalt. The lowest slopes of the mounds are often below annual high water mark and

Table 1. Numerical analysis of the Columbia Plateau vernal pool flora. The core flora omits any taxa that are uncommon, nonpersistent, and appear intolerant of the vernal pool flood or desiccation period.

Plant Type	Number of Species				
	All Taxa	Native Taxa	Core Natives	Non-native Taxa	Core Non-natives
Annual	157	132	111	25	16
Perennial	112	95	61	17	12
Woody	14	14	3	0	0
TOTAL	283	241	175	42	28

vernal pool species that prefer marginal areas typically form a distinct band of dense cover at mound base.

Vascular plant flora. Eighty-five percent of the 283 vascular plant taxa associated with the vernal pools were native (Table 1; Appendix). The 203 species that constituted the core vernal pool flora—taxa well adapted to the pool environment—included 28 non-natives and 175 natives. The core native flora was predominantly annual (63%), with abundant graminoids (45 taxa; 36 Poaceae) and composites (40 Asteraceae). Of the 14 woody taxa, all were native and only 3 were members of the core flora (*Eriogonum compositum*, *E. heracleoides*, and *Talinum spinescens*). The remaining woody taxa found were poorly adapted to flooding and were typically flood-killed.

The Columbia Plateau vernal pools have many floristic similarities to their California counterparts (Table 2). Thirty-four percent of the native taxa and 65% of the genera we found also occur in a comprehensive listing of California vernal pool taxa (Keeler-Wolf et al. 1998). The first author has recorded from Butte and Modoc Counties, California another seven native taxa shared between the two regions' vernal pools (*Carex athrostachya*, *Castilleja tenuis*, *Heterocodon rariflorum*, *Juncus hemiendytus* var. *hemiendytus*, *Myosurus clavicaulis*, and *Trifolium*

Table 2. Comparison of vascular plant taxon richness of vernal pools in California and on the Columbia Plateau of Washington. California figures are from the California Department of Fish and Game website (Keeler-Wolf et al. 1998).

Taxon Category	Number of Species		
	California	Columbia Plateau	Shared
Native genera	138	116	75
Native total taxa	367	224	77
Non-native total taxa	67	28	10

microcephalum). Ten of the 28 core non-native taxa are shared with the California vernal pools: *Amaranthus albus*, *Bromus hordaceus*, *Capsella bursa-pastoris*, *Convolvulus arvensis*, *Holosteum umbellatum*, *Polypogon monspeliensis*, *Rumex crispus*, *Spergularia bocconii*, *S. rubra*, and *Taeniatherum caput-medusae*.

Twenty-three of the most abundant and widespread taxa of the Columbia Plateau vernal pools have not been reported from vernal pools in California (Keeler-Wolf et al. 1998). Among these are *Achillea millefolium*, *Amsinckia* spp., *Artemisia ludoviciana* subsp. *ludoviciana*, *Camassia quamash* subsp. *quamash*, *Camissonia andina*, *Critesion jubatum*, *Cyperus squarrosus*, *Danthonia unispicata*, *Geranium bicknellii*, *Lagophylla ramosissima*, *Leymus cinereus*, *Lomatium bicolor* subsp. *leptocarpum*, *L. grayi*, *Madia* spp., *Microsteris gracilis*, *Montia dichotoma*, *M. linearis*, *Perideridia montana*, *Plantago patagonica*, *Poa scabrella*, *Sanguisorba occidentalis*, *Senecio hydrophiloides*, and *Trifolium cyathiferum*. Fifteen common and widespread non-natives have also not been reported from the California vernal pools, such as *Cirsium arvense*, *Elytrigia repens*, *Lactuca serriola*, *Poa compressa*, and *Sisymbrium altissimum*. Several core natives have not been found in California at all, including *Allium columbianum*, *A. geyeri* var. *geyeri*, *Camissonia hilgardii*, *Centaureum curvistamineum*, *Cirsium brevifolium*, *Clarkia pulchella*, *Delphinium distichum*, *Grindelia columbiana*, *Lomatium ambiguum*, *Microgilia micrantha*, *Navarretia leucocephala* subsp. *diffusa*, *Orthocarpus barbatus*, *O. tenuifolius*, *Polygonum polygaloides* subsp. *polygaloides*, and *Talinum spinescens*.

In Washington, many of the core native taxa are found almost exclusively in vernal pools. These include *Callitriche marginata*, *Camissonia tanacetifolia*, *Cuscuta* cf. *occidentalis*, *Elatine californica*, *E. chilensis*, *E. rubella*, *Juncus uncialis*, *Myosurus clavicaulis*, *Parietaria* cf. *hespera*, *Plagiobothrys* spp., *Polygonum polygaloides* subsp. *confertiflorum*, *P. polygaloides* subsp. *polygaloides*, *Psilocarphus brevissimus*, *P. elatior*, *P. oregonus*, *Trifolium cyathiferum*, and *Navarretia leucocephala* subsp. *diffusa*. The last of these was discovered and first described during this study (Björk 2002), and is endemic to the Columbia Plateau vernal pools. Other vernal pool taxa are disjunct from populations in vernal pools in the Columbia River Gorge or from farther south. These include *Alopecurus saccatus*, *Callitriche marginata*, *Downingia yina*, *Isoetes howellii*, *Juncus hemiendytus* var. *hemiendytus*, *J. uncialis*, *Myosurus clavicaulis*, *Navarretia leucocephala* subsp. *minima*, *Pilularia americana*, *Psilocarphus* spp., *Sclerolinon digynum*, and *Trichostema oblongum*.

Table 3. Per-pool taxon richness and total native richness reported from California pools and recorded in each subregion of the Columbia Plateau vernal pool province. Native and non-native richness values for east channel vernal pools are significantly different ($p < 0.01$) from those for west and central channel pools. *Barbour et al. 2003; Heise and Merenlender 1999; Holland 1976; Holland and Jain 1981. †Keeler-Wolf et al. 1998.

	Number of Species			
	California	Columbia Plateau, Washington		
		West Channel	Central Channel	East Channel
Per-pool richness				
Range	15–24*	20–51	22–86	12–59
Native (mean \pm 1 SE)		35.9 \pm 4.7	41.4 \pm 1.9	22.2 \pm 2.8
Non-native (mean \pm 1 SE)		6.0 \pm 1.0	4.7 \pm 0.4	2.8 \pm 0.5
Total native richness	367 [†]	221	181	136

Vernal pools in the central flood channels had the largest flora, followed by pools in the eastern and lastly, the western subregions (Table 3). Some members of the core flora were found only in a single channel. Limited to the west subregion were *Callitriche hermaphroditica*, *Lotus denticulatus*, and *Orthocarpus barbatus*. The taxa *Cyperus squarrosus*, *Gayophytum ramosissimum*, *Lilaea scilloides*, *Lomatium bicolor* subsp. *leptocarpum*, *Navarretia leucocephala* subsp. *diffusa*, and *Psilocarphus tenellus* were found in vernal pools only in the central subregion. Limited to the east subregion were *Allium columbianum*, *Centaureum curvistamineum*, *Downingia elegans*, *Juncus hemiendytus* var. *hemiendytus*, *Ranunculus alismifolius* var. *alismifolius*, *Sclerolinon digynum*, and *Trichostema oblongum*.

Pools on the Columbia Plateau had a higher species richness than those in California (Table 3). Native taxon richness was highest in the central subregion and lowest in the east. The eastern subregion pools also had the fewest non-native taxa per pool (2.88 ± 0.47), significantly fewer than the western (6.00 ± 0.98 ; $p = 0.0053$) and central (4.75 ± 0.41) subregions. The presence of rare taxa did not differ significantly between the subregions.

DISCUSSION

The Columbia Plateau vernal pool region is noteworthy for its plant diversity and large number of pools. Also, the pools occur within a steppe

and woodland vegetation mosaic that, overall, is in good condition compared to the communities surrounding most of the California vernal pools. Despite their biotic richness and geographic extent, it is surprising that they have received so little scientific attention. The paucity of herbarium specimens in WS and WTU collected from the Columbia Plateau pools also indicates how little attention these pools have received.

The physical environment of the Columbia Plateau vernal pools resembles that of vernal pools in California. Both regions exhibit extreme seasonality in precipitation, producing similar hydrological cycles in the pools. Vernal pools in both regions have shallow and relatively inorganic soils, low to moderate alkalinity and salt concentration, and minimal thatch and soil-organic matter. Pools in the two regions share many species and genera, and those of the Columbia Plateau are dominated by annuals just as are the California vernal pools (Holland and Jain 1988; Zedler 1987). Collectively, these characters distinguish these west-coast vernal pools from other seasonally inundated, closed-basin wetlands that are termed vernal pools in other regions.

Comparisons between vernal pools on the Columbia Plateau and in California reveal some significant differences. Vernal pools in the California Floristic Province contain more species limited to vernal pool ecosystems and contain far more endemic taxa than those on the Columbia Plateau. This higher level of endemism probably reflects the greater antiquity of the California pools as compared to those in Washington, which originated no earlier than the later Missoula Flood events. However, per-pool species richness observed in California (Barbour et al. 2003; Heise and Merenlender 1999; Holland 1976; Holland and Jain 1981; Björk, unpubl. data) is lower than in Washington.

Several floristic elements appear to be unique to the Columbia Plateau pools. At least two dozen taxa that have not been documented in vernal pools elsewhere are common in the core flora, although many of these taxa do occur in other habitats. Particularly noteworthy is the tolerance of these species to the flood/desiccation cycles of Washington vernal pools and apparently not to similar hydrological patterns in California vernal pools. Likewise unique is the endemic plant known from the Columbia Plateau vernal pools, *Navarretia leucocephala* subsp. *diffusa*.

Vernal pools on the Columbia Plateau appear to be less threatened than in California. In the former, pools occur mostly in basalt-bedrock landscapes, where most development and agriculture would be impractical. Hence, it appears that there has been little outright eradication of pools. In contrast, development and agriculture have reduced vernal pools in California to an estimated 10% of original pre-European settlement

levels (Ferren and Fiedler 1993). Estimates of regional losses range from 66% in the Central Valley (Holland 1978) and 95–97% in San Diego County (Bauder et al. 1998) to total loss in Los Angeles, Orange, Riverside, and San Bernardino Counties (United States Fish and Wildlife Service 1993). Threats from non-native species also have been less pronounced on the Columbia Plateau. Although non-native taxa have had a major impact on the landscape surrounding many vernal pools on the Columbia Plateau, few sites are completely dominated by non-natives as has happened in the grasslands surrounding most of California's vernal pools (Zedler 1987). Our observations in Washington suggest that these vernal pools have been generally less invaded by non-native taxa than the surrounding communities, a pattern also reported in California (Holland and Jain 1981; Zedler 1987). Only a small percentage of Columbia Plateau pools have been heavily impacted by non-natives, which contrasts with pools in California, where most are heavily impacted by non-natives such as *Anagallis arvensis*, *Cotula coronopifolia*, *Erodium* spp., *Lolium* spp., *Lythrum hyssopifolium*, *Mentha pulegium*, *Polypogon* spp., and *Taeniatherum caput-medusae* (Barry 1998; Keeler-Wolf et al. 1998; Zedler 1987).

The extensive array of vernal pools in Washington represents a biologically significant resource that has been largely overlooked. Our investigations have uncovered numerous occurrences of plant species previously unrecorded in Washington. Given the lack of recognition of these habitats in the published literature, it is likely that there remain similar discoveries to be made among the very rich fauna that also occur in these systems. Future investigations of vernal pool biogeography, ecology, floristics, and fauna on the Columbia Plateau should encompass these important habitats.

ACKNOWLEDGMENTS. We thank the many public and private landholders who facilitated access to the vernal pools, including the Washington Department of Fish and Wildlife, the Bureau of Land Management, and the United States Fish and Wildlife Service.

LITERATURE CITED

- ANGIOSPERM PHYLOGENY GROUP. 1998. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.
- BARBOUR, M., A. SOLOMESHCH, C. WITHAM, R. HOLLAND, R. MACDONALD, S. CILLIERS, J. A. MOLINA, J. BUCK, AND J. HILLMAN. 2003. Vernal pool vegetation of California: Variation within pools. *Madroño* 50: 129–146.
- BARRY, S. J. 1998. Managing the Sacramento Valley vernal pool landscape to sustain the native flora, pp. 236–240. *In*: C. W. Witham, E. T. Bauder, D. Belk,

- W. R. Ferren, Jr., and R. Ornduff, eds., Ecology, Conservation, and Management of Vernal Pool Ecosystems: Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA.
- BAUDER, E. T., D. A. KRAEGER, AND S. MACMILLAN. 1998. Vernal Pools of Southern California: Recovery Plan. U.S. Fish Wild. Service, Portland, OR.
- BJÖRK, C. R. 2002. A new subspecies of *Navarretia leucocephala* (Polemoniaceae) from vernal pools in eastern Washington. *Madroño* 49: 165–168.
- BRETZ, J. H. 1969. The Lake Missoula floods and the channeled scabland. *J. Geol.* 77: 505–543.
- BROWN, W. L. 2001. Eastern Washington vernal pools: Ecology and conservation, pp. 144–150. *In*: S. H. Reichard, P. Dunwiddie, J. Gamon, A. Kruckeberg, and D. Salstrom, eds., Conservation of Washington's Rare Plants and Ecosystems. Washington Native Plant Society, Seattle, WA.
- CROWE, E. A., A. J. BUSACCA, J. P. REGANOLD, AND B. A. ZAMORA. 1994. Vegetation zones and soil characteristics in vernal pools in the Channeled Scabland of eastern Washington. *Great Basin Naturalist* 54: 234–247.
- FERREN, W. R., JR. AND P. L. FIEDLER. 1993. Rare and threatened wetlands of central and southern California, pp. 119–131. *In*: J. E. Keeley, ed., Interface Between Ecology and Land Development in Southern California. Southern California Acad. Sci., Los Angeles, CA.
- HEISE, K. L. AND A. M. MERENLENDER. 1999. Flora of a vernal pool complex in the Mayacmas Mountains of southeastern Mendocino County, California. *Madroño* 46: 38–45.
- HICKMAN, J. C., ed. 1993. The Jepson Manual of the Higher Plants of California. Univ. California Press, Berkeley, CA.
- HOLLAND, R. F. 1976. The vegetation of vernal pools: A survey, pp. 11–15. *In*: S. K. Jain, ed., Vernal Pools: Their Ecology and Conservation. Institute of Ecology Publ. No. 9, Univ. California, Davis, CA.
- . 1978. Vernal pools: The geographic and edaphic distribution of vernal pools in the Central Valley of California. California Native Plant Society, Sacramento, CA.
- AND S. K. JAIN. 1981. Insular biogeography of vernal pools in the Central Valley of California. *Amer. Naturalist* 117: 24–37.
- AND ———. 1988. Vernal pools, pp. 513–533. *In*: M. Barbour and J. Major, eds., Terrestrial Vegetation of California. Wiley Interscience, New York.
- JAIN, S. K. AND P. MOYLE, eds. 1984. Vernal pools and Intermittent Streams. Institute of Ecology Publ. No. 28, Univ. California, Davis, CA.
- KEELER-WOLF, T., D. R. ELAM, K. LEWIS, AND S. A. FLINT. 1998 [modified 2000]. Plant species associated with vernal pools [website]. *In*: California Vernal Pool Assessment. Preliminary Report, Appendix C. California Dept. Fish Game, Sacramento, CA. Website (http://maphost.dfg.ca.gov/wetlands/vp_asses_rept/app_c_plnt.htm). Accessed 27 July 2000.
- PURER, E. 1939. Ecological study of vernal pools, San Diego County. *Ecology* 20: 217–229.
- UNITED STATES DEPARTMENT OF COMMERCE. 1973. Climates of the United States. U.S. Dept. Commerce, Washington, DC.
- UNITED STATES FISH AND WILDLIFE SERVICE. 1993. Endangered and threatened wildlife and plants: Final rule: Determination of endangered status for three vernal pool plants and the Riverside fairy shrimp. *Fed. Reg.* 58: 4139.

- WITHAM, C. W., E. T. BAUDER, D. BELK, W. R. FERREN, JR., AND R. ORNDUFF, eds. 1998. Ecology, Conservation, and Management of Vernal Pool Ecosystems: Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA.
- ZEDLER, P. H. 1987. The Ecology of Southern California Vernal Pools: A Community Profile. Biol. Report 85(7.11), U.S. Fish Wild. Service, U.S. Dept. Interior, Washington, DC.

APPENDIX

SPECIES OF THE COLUMBIA PLATEAU VERNAL POOLS

Plant taxa of the Columbia Plateau vernal pools recorded in the 1997–1998 seasons. The symbols W, C, and E following the notes on each taxon indicate occurrence in the west, central, and east subregions, respectively. Non-core applies to taxa that are intolerant of the flood/desiccation cycle of vernal pools and which occurred as accidentals below the highest observed water levels. Non-native taxa are preceded by an asterisk (*). Collection numbers are those of the first author.

ISOETALES

ISOETACEAE. *Isoetes howellii* Engelm. – Occasional to locally common on basins; W, C, E.

FILICALES

DRYOPTERIDACEAE. *Woodsia oregana* D.C. Eaton – Rare on pool margins; flood-intolerant; non-core; W.

MARSILEACEAE. *Marsilea oligospora* Goodd. – Rare on basins; appears to be annual in vernal pools; C; 1259 (ws), 3233 (WTU). *Marsilea vestita* Hook. & Grev. – Occasional on basins; appears to be annual in vernal pools; C, E. *Pilularia americana* A. Br. – Rare on pool basins; C, E; 1261 (ws), 3287 (WTU).

ANTHOPHYTES

MONOCOTS

ALISMATACEAE. *Alisma gramineum* C.C. Gmel. – Rare in deep areas of large pools, where possibly annual; W, C, E. *Alisma triviale* Pursh – Rare in deep areas of large pools, where possibly annual; E. *Sagittaria cuneata* E. Sheldon – Rare in deep areas of large pools, where possibly annual; W.

ALLIACEAE. *Allium acuminatum* Hook. – Uncommon on margins; non-core; W, C, E. *Allium columbianum* (Ownbey & Mingrone) P.M. Peterson, Annable & Rieseberg – Locally common in shallow pools; on both margins and basins, less common in dry

uplands than in pools; E. *Allium geyeri* S. Watson var. *geyeri* – Very common on both margins and basins; W, C, E.

CYPERACEAE. *Bolboschoenus maritimus* (L.) Palla – Rare on basins of deep or expansive pools; W. *Carex athrostachya* Olney – Occasional on margins and basins; W, C, E. *Carex douglasii* Boott – Occasional on margins and basins where alkaline/salty; W, C, E. *Carex petasata* Dewey – Uncommon on pool margins, mostly where moderately alkaline; W. *Carex praegracilis* Boott – Uncommon on margins of alkaline pools; E. *Cyperus squarrosus* L. – Locally very common on basins, especially in the central subregion; C. *Eleocharis acicularis* (L.) Roem. & Schult. – Very common on basins, especially in deepest areas of pools; W, C, E. *Eleocharis bella* (Piper) Svenson – Rare on pool basins; C, E. *Eleocharis macrostachya* Britton – Very common in nearly all vernal pools, mostly on basins but sometimes spreading to margins; W, C, E. *Eleocharis parvula* (Roem. & Schult.) Link ex Bluff, Nees & Schauer – Rare on pool basins; W.

HYACINTHACEAE. *Camassia quamash* (Pursh) E. Greene var. *quamash* – Common on basins and margins; W, C, E.

IRIDACEAE. *Iris missouriensis* Nutt. – Occasional on margins, more common in more permanently moist areas like swales; C, E. *Sisyrinchium douglasii* A. Dietr. var. *inflatum* (Suksd.) P.K. Holmgr. – Occasional on margins; E. *Sisyrinchium halophilum* E. Greene – Occasional on margins of alkaline/salty pools, more common on salt flat margins; non-core; C; 6207 (ws). *Sisyrinchium idahoense* E.P. Bicknell – Occasional on margins; non-core; C.

JUNCACEAE. *Juncus acuminatus* Michx. – Occasional on margins; E. *Juncus arcticus* Willd. var. *mexicanus* (Willd. ex Schult. & Schult. f.) Balslev – Common on margins; W, C, E. *Juncus bufonius* L. var. *bufonius* – Very common on basins; W, C, E. *Juncus bufonius* L. var. *occidentalis* F.J. Herm. – Less common than var. *bufonius* and usually growing with it; W, C, E; 3033 (ws), 3227, 3286 (WTU). *Juncus dudleyi* Wieg. – Occasional on margins; C, E. *Juncus hemiendytus* F.J. Herm. var. *hemiendytus* – Rare on basins; E; 3037, 3205, 3214 (WTU). *Juncus nevadensis* S. Watson – Uncommon on margins; W, C. *Juncus uncialis* E. Greene – Rare on basins; W, C, E; 3038 (ws), 3036, 3209, 3289, 3314 (WTU).

JUNCAGINACEAE. *Lilaea scilloides* (Poir.) Hauman – Rare on basins in mostly large pools; C; 1895 (ws).

POACEAE. *Achnatherum thurberianum* (Piper) Barkworth – Rare on margins; non-core; C. *Agrostis diegoensis* Vasey – Common on margins, uncommon on basins; W, C, E. *Agrostis exarata* Trin. – Uncommon on margins; C. **Agrostis stolonifera* L. – Uncommon on margins, usually where alkaline/salty; C. *Alopecurus carolinianus* Walter – Common on basins; C, E; 3158 (WTU). *Alopecurus saccatus* Vasey – Common on basins; intergrading with *A. carolinianus*; W, C, E; 3327 (WTU), 3886, 6198 (ws). **Apera interrupta* (L.) P. Beauv. – Very common on margins; one of the most abundant plants seen in the region in the cool, wet 1997 season, but dramatically less common in the dry, hot 1998 season; W, C, E. *Beckmannia sizygapne* (Steud.) Fernald – Occasional on basins; E. **Bromus hordaceus* L. – Very common on

margins; W, C, E. **Bromus tectorum* L. – Uncommon on margins; apparently flood-intolerant; W, C, E. *Calamagrostis rubescens* Buckley – Locally common around margins; E. *Critesion californicum* (Covas & Stebbins) Á. Löve – Common on margins and basins; W, C, E; 6210 (ws). *Critesion depressum* (Scribn. & J.G. Sm.) Á. Löve – Uncommon on margins and basins; W, C. *Critesion jubatum* (L.) Nevski – Common on margins and basins; W, C, E. *Danthonia californica* Bol. subsp. *californica* – Occasional on margins; E. *Danthonia unispicata* (Thurb.) Munro ex Macoun – Common on margins, occasional on basins; W, C, E. *Deschampsia cespitosa* (L.) P. Beauv. – Uncommon on margins; E. *Deschampsia danthonioides* (Trin.) Munro ex Benth. – Very common on basins, but mostly not in pool center; W, C, E. *Distichlis spicata* (L.) E. Greene – Common on basins and margins of alkaline/salty pools; W, C; 6211 (ws). *Elymus elymoides* (Raf.) Swezey – Occasional on margins, uncommon on basins; C, E. **Elytrigia repens* (L.) Desv. ex B.D. Jacks. – Common in disturbed pools, growing on basins and margins; W, C, E. *Festuca idahoensis* Elmer – Common near margins, but not flood-tolerant; non-core; C. *Festuca rubra* L. Common near margins, flood-intolerant; non-core; C. *Leymus cinereus* (Scribn. & Merr.) Á. Löve – Very common on margins; W, C, E. *Leymus* sp. – One population on the floor of a very large pool; C; 3252 (wtu). *Muhlenbergia asperifolia* (Nees & Meyen ex Trin.) Parodi – Occasional in alkaline/salty pools; C. *Muhlenbergia richardsonis* (Trin.) Rydb. – Common on basins and margins; W, C, E. *Panicum capillare* L. – Common on basins and margins, germinating post-desiccation; C, E. *Pascopyrum smithii* (Rydb.) Barkworth & D.R. Dewey – Uncommon on basins and margins, mostly in alkaline/salty pools; C. **Phalaris arundinacea* L. – Occasional on margins and basins of disturbed pools; E. **Phleum pratense* L. – Uncommon on margins and basins, probably growing only where sowed for forage; E. **Poa bulbosa* L. – Common on margins; W, C, E. **Poa compressa* L. – Common on basins of east subregion pools, in both disturbed and pristine pools; W, C, E. *Poa juncifolia* Scribn. – Rare on margins of alkaline/salty pools; non-core; C. **Poa pratensis* L. – Uncommon on margins and basins, mostly where disturbed; W, E. *Poa scabrella* (Thurb.) Benth. ex Vasey – Very common on margins, uncommon on basins; W, C, E. **Polypogon monspeliensis* (L.) Desf. – Common on margins and basins of alkaline/salty pools; W, C. *Pseudoroegneria spicata* (Pursh) Á. Löve – Flood intolerant, occasional along pool margins; non-core; W, C, E. **Puccinellia distans* (Jacq.) Parl. – Occasional on margins and basins of alkaline/salty pools; W; 3200 (wtu). *Puccinellia nuttalliana* (Schult.) Hitchc. – Occasional on margins and basins of alkaline/salty pools; C. *Sphenopholis obtusata* (Michx.) Scribn. – Rare on basins, limited to alkaline/salty pools; C. **Taeniatherum caput-medusae* (L.) Nevski – Locally common on margins; W, C, E. **Triticum* cultivar (seedlings) – Uncommon on basins, mostly in roadside pools; germinating post-desiccation and never reaching maturity; intolerant of summer drought; non-core; C, E. *Vulpia octoflora* (Walter) Rydb. – Rare on margins; non-core; C.

POTAMOGETONACEAE. *Stuckenia pectinata* (L.) Börner – Rare on basins of deep, alkaline/salty pools; W.

TYPHACEAE. *Typha latifolia* L. (seedlings only) – Occasional on basins; always dying from drought in the first season before reaching maturity; non-core; C, E.

ZANNICHELLIACEAE. *Zannichellia palustris* L. – Rare in deep pools; W.

EUDICOTS

AMARANTHACEAE. **Amaranthus albus* L. – Occasional summer annual on pool basins, germinating post-desiccation; W, C, E. *Amaranthus californicus* (Moq.) S. Watson – Locally common on pool basins; E. *Amaranthus graezicans* S. Watson – Common summer annual of pool basins, germinating post-desiccation; W, C, E. *Atriplex truncata* (Torr. ex S. Watson) A. Gray – Occasional in alkaline/salty pools; W, C. *Chenopodium rubrum* L. – Rare on basins in alkaline/salty pools; C. *Chenopodium* sp. (*C. album* complex) – Occasional on margins; non-core; E. *Monolepis nuttalliana* (Schult.) E. Greene – A single plant found on a post-desiccation pool floor; C. *Suaeda calceoliformis* (Hook.) Moq. – Rare on margins of alkaline/salty pools; C.

APIACEAE. *Lomatium ambiguum* (Nutt.) J.M. Coult. & Rose – Occasional on margins; common on Mima mounds surrounding vernal pools; non-core; W, C, E. *Lomatium bicolor* (S. Watson) J.M. Coult. & Rose subsp. *leptocarpum* (Nutt. ex Torr. & A. Gray) Schlessman – Locally common on margins and basins; C; 3391 (ws). *Lomatium grayi* (J.M. Coult. & Rose) J.M. Coult. & Rose – Locally common on margins and basins; equally common in pools and in surrounding grasslands; W, C, E. *Lomatium macrocarpum* (Nutt. in Torr. & A. Gray) J.M. Coult. & Rose – Occasional on margins; flood-intolerant; non-core; W, C, E. *Perideridia montana* (Blank.) Dorn – Common on margins in all three subregions, very common on Mima mounds surrounding vernal pools; W, C, E.

APOCYNACEAE. *Asclepias speciosa* Torr. – Rare on margins; non-core; W, C, E.

ASTERACEAE. *Achillea millefolium* L. – Common on margins, occasional on basins; the local form is flood-tolerant; W, C, E. *Agoseris grandiflora* (Nutt.) E. Greene – Occasional on margins, locally common on Mima mounds surrounding vernal pools; non-core; C. *Agoseris heterophylla* (Nutt.) E. Greene – Occasional, mostly on margins; W, C, E. *Ambrosia* sp. – A single occurrence on margins of an alkaline pool; non-core; E. *Antennaria luzuloides* Torr. & A. Gray – Rarely found on pool margins, very common on surrounding lithosol; flood-intolerant; non-core; E. *Antennaria stenophylla* (A. Gray) A. Gray – Rare on pool margins; flood-intolerant; non-core; C. *Arnica fulgens* Pursh – Rare on margins, occasional in surrounding grassland; non-core; C (W, E?). *Arnica sororia* E. Greene – Rare on margins, occasional in surrounding grassland; non-core; W, E (C?). *Artemisia biennis* Willd. – Occasionally found in alkaline pools; W, C. *Artemisia ludoviciana* Nutt. var. *ludoviciana* – Common on margins and basins; flood-tolerant; W, C, E. *Artemisia rigida* (Nutt.) A. Gray – Rare on margins, common on lithosol surrounding rocky pools, flood-intolerant; non-core; C. *Artemisia tridentata* Nutt. subsp. *tridentata* – Common around pools; flood intolerant, germinates occasionally in pools post-desiccation and with the first fall rains, but is later killed in high water; W, C, E. *Artemisia tripartita* Rydb. – Rare on margins, flood-intolerant; non-core; C. **Centaurea* spp. – Rare on margins, mostly where disturbed; common in local outbreaks in surrounding grassland, mostly where grazing is heavy; non-core; W. *Chamomilla suaveolens* (Pursh) Rydb. – Occasional on pool basins and margins; often very robust and semi-succulent when growing in alkaline/salty pools; C, E. *Chrysothamnus nauseosus* (Pall. ex Pursh) Britton – Rare on margins; flood-intolerant; C. **Cirsium arvense* (L.) Scop. – Occasional on margins and

basins, mostly where disturbed; moderately flood-tolerant; W, C, E. *Cirsium brevifolium* Nutt. – Occasional on pool margins, more common beyond pool margins on tops of Mima mounds; apparently tolerant of brief flooding; C, E. **Cirsium vulgare* (Savi) Ten. – Uncommon on pool margins, mostly where disturbed; non-core; W, C, E. *Conyza canadensis* (L.) Cronq. – Common on margins and basins, germinating post-desiccation; W, C, E. *Erigeron corymbosus* Nutt. – Rare on margins; non-core; C. *Erigeron pumilus* Nutt. subsp. *intermedius* Cronq. var. *gracilior* Cronq. – Rare on margins; flood-intolerant; non-core; C, E. **Filago arvensis* L. – Uncommon on margins; C, E. *Gaillardia aristata* Pursh – Occasional on margins, common on Mima mounds surrounding vernal pools; flood intolerant; non-core; W, C, E. *Gnaphalium palustre* Nutt. – Very common on basins, occasional on margins; W, C, E. *Grindelia columbiana* (Piper) Rydb. – Common in central and west subregions, on basins and margins, equally common in pools and in surrounding grasslands; possibly just a rayless form of *G. nana*; W, C. *Grindelia nana* Nutt. – Common on basins and margins, equally common in pools and in surrounding grasslands; C, E. *Helianthus annuus* L. – Occasional, germinating on basins post-desiccation; usually dies from drought before flowering; W, E. *Iva axillaris* Pursh – Occasional on margins of alkaline/salty pools, much more common in and around more permanent wetlands; W, C. **Lactuca serriola* L. – Common on margins and basins, mostly germinating post-desiccation; highly drought-tolerant, flowering well into autumn; W, C, E. *Lactuca tatarica* (L.) C.A. Mey. subsp. *pulchella* (Pursh) Stebb. – Rare on margins, more common on Mima mounds surrounding vernal pools; non-core; C, E. *Lagophylla ramosissima* Nutt. – Common on margins, more so than in surrounding grasslands; C. *Madia exigua* (Sm.) A. Gray – Very common on margins; typically growing at higher densities on pool margins than in surrounding grasslands; W, C, E. *Madia glomerata* Hook. – Common on margins; typically growing at higher densities on pool margins than in surrounding grasslands; W, C, E. *Madia gracilis* (Sm.) D.D. Keck – Common on margins; typically growing at higher densities on pool margins than in surrounding grasslands; C, E. *Microseris nutans* (Hook.) Sch.Bip. – Occasional on margins; flood-intolerant; non-core; C. *Nothocalais troximoides* (A. Gray) E. Greene – Rare on margins; non-core; C. *Psilocarphus brevissimus* Nutt. – Very common on pool basins; often intergrading with *P. elatior*; W, C, E. *Psilocarphus elatior* A. Gray – Very common on pool basins; often intergrading with *P. brevissimus*; C, E. *Psilocarphus oregonus* Nutt. – Very common on pool basins; W, C, E; 3216 (WTU). *Psilocarphus tenellus* Nutt. – Rare; found in only two pools, both having unusual cherty-clay soil; C, E; 3390 (WTU). *Senecio hydrophiloides* Rydb. – Common on margins, locally very common in seasonally wet meadows surrounding vernal pools; C, E. *Senecio integerrimus* Nutt. – Occasional on margins, common on Mima mounds surrounding vernal pools; non-core; C, W. *Senecio serra* Hook. – Occasional on margins, very common on Mima mounds surrounding vernal pools; non-core; C. **Sonchus asper* (L.) Hill – Occasional on margins and basins, germinating post-desiccation; C. **Taraxacum officinalis* Weber ex F.H. Wigg. – Rare on margins; flood-intolerant; common in surrounding grasslands where heavily grazed; non-core; W, C, E. **Tragopogon dubius* Scop. – Occasional on margins; non-core; C, W. *Xanthium strumarium* L. – Rare on basins, germinating post-desiccation; W.

BORAGINACEAE. *Amsinckia lycopsoides* Lehm. – Common on margins, growing at higher densities on pool margins than in surrounding grasslands; W, C, E. *Amsinckia menziesii* (Lehm.) A. Nels. & J.F. Macbr. var. *intermedia* (Fischer & C.A. Mey.)

Ganders – Occasional on margins, more common on Mima mounds surrounding vernal pools; C, E. *Amsinckia menziesii* (Lehm.) A. Nels. & J.F. Macbr. var. *menziesii* – Occasional on margins, more common on Mima mounds surrounding vernal pools; C, E. *Amsinckia retrorsa* Suksd. – Common on margins, growing at higher densities on pool margins than in surrounding grasslands; W, C, E. **Anchusa officinalis* L. – Rare on margins; non-core; E. *Cryptantha torreyana* (A. Gray) E. Greene – Occasional on margins; W, C, E. *Hesperochiron californicus* (Benth.) S. Watson – Occasional on margins, mostly around alkaline/salty pools; W, C, E. *Lappula redowskii* (Hornem.) E. Greene – Occasional on margins; flood-intolerant; non-core; C. **Lithospermum arvense* L. – Rare on margins; flood-intolerant; non-core; E. **Myosotis micrantha* Pall. ex Lehm. – Occasional on margins; C, E. *Myosotis verna* Nutt. – Occasional on margins, more common on Mima mounds and lithosols surrounding vernal pools; C, E. *Plagiobothrys leptocladus* (E. Greene) I.M. Johnston – Very common on basins, commonest in west and central subregions; W, C, E. *Plagiobothrys* spp. [*P. bracteatus* (T.J. Howell) I.M. Johnston; *P. cognatus* (E. Greene) I.M. Johnston; *P. cusickii* (E. Greene) I.M. Johnston, 1675, 1676 (ws); *P. hispidulus* (E. Greene) I.M. Johnston; *P. scouleri* (Hook. & Arn.) I.M. Johnston; *P. stipitatus* (E. Greene) I.M. Johnston, 1670 (ws); *P. tener* (E. Greene) I.M. Johnston, 1669 (ws)] – Locally very common; more work is needed to sort out the diversity of this complex in the Columbia Plateau pools, fragrance as well as corolla size and coloration in at least some populations vary between wet/cool and hot/dry climatic periods; W, C, E.

BRASSICACEAE. *Arabis nuttallii* B.L. Rob. – Rare on margins, more common in swales and wet meadows; C. *Arabis sparsiflora* Nutt. – Rare on margins; flood-intolerant; non-core; C. *Barbarea orthoceras* Ledeb. – Locally common on margins and basins; E. **Capsella bursa-pastoris* (L.) Medik. – Rare on margins; non-core; C. *Cardamine oligosperma* Nutt. – Rare on margins and basins; E. **Descurainia sophia* (L.) Webb in Engl. & Prantl – Occasional on margins, mostly where disturbed; non-core; C. *Draba verna* L. – Occasional on margins; flood-intolerant; very common beyond high water mark on both lithosols and deeper soils surrounding vernal pools; W, C, E. *Erysimum cheiranthoides* L. – Rare on pool basins; E. *Idahoia scapigera* (Hook.) A. Nels. & J.F. Macbr. – Occasional on margins, much more common on winter-wet lithosols surrounding vernal pools; C, E. **Lepidium perfoliatum* L. – Occasional on margins, most common where alkaline/salty; W, C, E. *Lepidium* spp. – Rare on margins; non-core; W. *Rorippa curvisiliqua* (Hook.) Bessey ex Britton – Very common on basins; germinating both pre- and post-desiccation and acting either as an annual or a biennial; W, C, E. **Sisymbrium altissimum* L. – Common on margins, particularly where disturbed; flood-intolerant; G; germinating post-desiccation; very common in surrounding grasslands, especially where disturbed; non-core; W, C, E.

CAMPANULACEAE. *Downingia elegans* (Dougl. ex Lindl.) Torr. – Common on basins; E. *Downingia yina* Applegate – Common on basins, mostly in west and central subregions; highly variable throughout the full range, but uniform across the Columbia Plateau; W, C, E; 3282, 3443 (WTU). *Heterocodon rariflorum* Nutt. – Occasional on margins and basins; C, E.

CAPRIFOLIACEAE. *Symphoricarpos albus* (L.) S.F. Blake – Rare on margins, flood-intolerant; non-core; C, E.

CARYOPHYLLACEAE. *Cerastium nutans* Raf. – Occasional on margins; W, C, E. **Holosteum umbellatum* L. – Occasional on margins; very common in surrounding grasslands; W, C, E. **Spergularia bocconii* (Scheele) Foucaud – Occasional on basins; W, C, E. *Spergularia maritima* (All.) Chiov. – Very common on basins; C, E. **Spergularia rubra* (L.) J. Presl & C. Presl – Rare on basins and margins; W.

CLUSIACEAE. **Hypericum perforatum* L. – Rare on margins; locally very common in surrounding grasslands, particularly on Mima mounds surrounding vernal pools; non-core; E.

CONVOLVULACEAE. **Convolvulus arvensis* L. – Locally common on basins and margins; E. *Cuscuta occidentalis* Millsp. – Uncommon, most often on margins, but apparently never in upland areas beyond the pools; parasitizes a wide variety of hosts; W, C; 3156, 3369 (WTU).

ELATINACEAE. *Elatine californica* A. Gray – Occasional on pool basins; W, C, E. *Elatine chilensis* Gay and/or *E. rubella* Rydb. – Rare on pool basins; C, E; 1383 (ws).

EUPHORBIACEAE. *Chamaesyce serpyllifolia* (Pers.) Sm. – Common on pool basins, germinating post-desiccation; W, C, E.

FABACEAE. *Astragalus agrestis* Dougl. ex Hook. – Occasional on margins, mostly where alkaline/salty; C. *Lotus denticulatus* (Drew) E. Greene – Locally common on margins; W; 1498 (ws). *Lotus purshiana* (Benth) F. Clements & E. Clements – Very common on margins; W, C, E. *Lupinus* spp. – Uncommon on margins; all local species apparently flood-intolerant; very common in surrounding grasslands; non-core; W, C. **Medicago lupulina* L. – Occasional on margins, and germinating on basins post-desiccation; flood-intolerant; non-core; W, C, E. **Melilotus* spp. – Uncommon on margins and germinating on basins post-desiccation; flood-intolerant; apparently always dying of drought in vernal pools before the end of summer; non-core; W, C, E. *Trifolium cyathiferum* Lindl. – Common on margins; W, C, E. **Trifolium dubium* Sibth. – Uncommon on margins; apparently flood-intolerant; non-core; W, C, E. *Trifolium microcephalum* Pursh – Common on margins; W, C, E. *Trifolium variegatum* Nutt. ex Torr. & A. Gray – Common on margins; W, C, E. **Vicia villosa* Roth – Rare on margins; C, E.

GENTIANACEAE. *Centaurium curvistamineum* (Wittr.) Abrams – Locally common on basins and margins; E; 3441 (WTU). *Centaurium exaltatum* (Griseb.) W. Wight ex Piper – Occasional on basins and margins of alkaline/salty pools; W, C.

GERANIACEAE. *Geranium bicknellii* Britton – Common on basins and margins; germinating post-desiccation; W, C, E.

GROSSULARIACEAE. *Ribes cereum* Dougl. var. *cereum* – Rare on margins, flood-intolerant; non-core; C.

LAMIACEAE. *Mentha arvensis* L. – Rare on margins mostly of very large pools; flood-tolerant, but apparently not highly tolerant of the drought stage in vernal pools;

C. Trichostema oblongum Benth. – Rare in small, cobbly pools; E; 3221 (WTU), 6212 (ws).

LINACEAE. *Linum lewisii* Pursh – Uncommon on margins; non-core; *C. Sclerolinon digynum* (A. Gray) C.M. Rogers – Rare on margins; E; 3222, 3447 (WTU), 6208 (ws).

LOASACEAE. *Mentzelia dispersa* S. Watson – Rare on margins; non-core; E.

LYTHRACEAE. *Ammannia robusta* Heer & Regel – Rare on pool basins in the east subregion; non-core; found only in two pools adjacent to permanent lakes; E; 3451 (WTU).

MALVACEAE. *Sidalcea oregana* (Nutt. ex Torr. & A. Gray) A. Gray var. *maxima* (M.E. Peck) C.L. Hitchc. – Occasional on margins; plants of some populations around western pools are very robust, producing stout horizontal rhizomes and growing as tall as 1.5 m; W, C. *Sidalcea oregana* (Nutt. ex Torr. & A. Gray) A. Gray var. *procera* C.L. Hitchc. – Occasional on margins; W, C, E.

MYRSINACEAE. *Anagallis minima* (L.) E.H.L. Krause – Occasional on basins and margins, particularly where alkaline/salty; W, C, E; 3223 (WTU).

ONAGRACEAE. *Boisduvalia densiflora* (Lindl.) S. Watson – Very common on basins and margins; W, C, E. *Boisduvalia glabella* (Nutt.) Walp. – Very common on basins, especially in deep areas; W, C, E. *Boisduvalia stricta* (A. Gray) E. Greene – Uncommon on basins and margins; W, C, E. *Camissonia andina* (Nutt.) P.H. Raven – Occasional on basins and margins; C, E. *Camissonia hilgardii* (E. Greene) P.H. Raven – Rare on basins and margins; may be just a large-flowered form of *C. andina*; W, C; 1554 (ws), 3286 (WTU). *Camissonia tanacetifolia* (Torr. & A. Gray) P.H. Raven – Occasional on basins; C, E; 1555 (ws). *Clarkia pulchella* Pursh – Common on margins; very abundant in 1997 but far less so in 1998; W, C, E. *Epilobium brachycarpum* C. Presl – Very common on margins; W, C, E. *Epilobium* spp. – Occasional on margins; W, C. *Gayophytum ramosissimum* Torr. & A. Gray – Rare on basins of pools having cherty-clay soil; C.

OROBANCHACEAE. *Castilleja minor* (A. Gray) A. Gray subsp. *minor* – Occasional on margins where alkaline/salty; W, C; 3446 (WTU). *Castilleja tenuis* (A.A. Heller) Chuang & Heckard – Very common on margins, uncommon on basins; W, C, E; 6192 (ws). *Orthocarpus barbatus* J.S. Cotton – Uncommon on margins; W. *Orthocarpus tenuifolius* (Pursh) Benth. – Common on margins; W, C, E.

PHRYMATACEAE. *Mimulus breviflorus* Piper – Occasional on margins and basins; W, C, E. *Mimulus floribundus* Dougl. ex Lindl. – Occasional on margins, grows extremely robustly around alkaline/salty pools; W, C; 3334 (WTU). *Mimulus guttatus* Fisch. ex DC. – Occasional on margins; unlike in California, the Scabland form of this species does not appear to tolerate the pool-floor habitat; W, C, E. *Mimulus suksdorfii* A. Gray – Rare on margins; W; 3283 (WTU).

PLANTAGINACEAE. *Callitriche hermaphroditica* L. – Found only in one moderately alkaline pool in the Grand Coulee; W. *Callitriche marginata* Torr. – Uncommon on

basins, mostly in deep or expansive pools; C, E; 1693 (ws), 3288 (WTU). *Collinsia parviflora* Dougl. ex Lindl. – Occasional on margins; E. *Gratiola ebracteata* Benth. – Common on basins; C, E. *Gratiola neglecta* Torr. – Rare on basins; E. *Limosella aquatica* L. – Very common on basins; W, C, E. *Penstemon procerus* Dougl. ex Graham – Rare on margins; non-core; C, E. **Plantago major* L. – Uncommon on margins and basins; native in part; C. *Plantago patagonica* Jacq. – Very common, mostly on margins; W, C, E. **Veronica arvensis* L. – Rare on margins; non-core; E. *Veronica peregrina* L. var. *xalapensis* Kunth – Very common, mostly on basins; W, C, E.

POLEMONIACEAE. *Collomia linearis* Nutt. – Uncommon on margins; non-core; C, E. *Microgilia minutiflora* (Benth.) J.M. Porter & L.A. Johnson – Rare on basins of pools having a cherty-clay soil; C. *Microsteris gracilis* (Hook.) E. Greene – Very common on margins, especially in the east subregion; sometimes forming dense populations of tall, robust plants having relatively large, fragrant flowers; W, C, E. *Navarretia intertexta* (Benth.) Hook. – Common on margins; subspp. *intertexta* and *propinqua* intergrade locally, and some populations cannot be assigned to one or the other subspecies; W, C, E; 3231 (WTU). *Navarretia leucocephala* Benth. subsp. *diffusa* Björk – Very common on basins only in central Lincoln County (the northern central-subregion pools), where growing to the exclusion of subsp. *minima*; C; 3228, 3250 (WTU). *Navarretia leucocephala* Benth. subsp. *minima* (Nutt.) A.G. Day – Very common on basins, not occurring in the range of subsp. *diffusa*; W, C (southern portions), E; 3204 (WTU). *Phlox longifolia* Nutt. – Rare on margins; flood-intolerant; non-core; W, C.

POLYGONACEAE. *Eriogonum compositum* Dougl. ex Benth. – Occasional on margins of central and east subregion pools, where the local form is flood-tolerant; C, E. *Eriogonum heracleoides* Nutt. – Occasional on margins, especially in the west subregion pools; the local form is flood-tolerant; W, C, E. *Eriogonum niveum* Dougl. ex Benth. – Rare on margins, apparently flood-intolerant; non-core; C. *Eriogonum thymoides* Benth. – Uncommon on margins of the central and west subregion pools; apparently flood-intolerant; non-core; C. *Polygonum achoreum* S.F. Blake – Very common on basins and margins; germinating post-desiccation; W, C, E. *Polygonum douglasii* E. Greene subsp. – Uncommon on margins; flood intolerant; non-core; W, C, E. *Polygonum polygaloides* Meisn. subsp. *confertiflorum* (Nutt. ex Piper) J.C. Hickman – Very common on basins and margins, especially in the central and west subregions [some populations in eastern pools may be attributable to subsp. *esotericum* (L.C. Wheeler) J.C. Hickman, a rare regional endemic of northern California; wider sampling is needed to determine the identity of these populations]; W, C, E; 1362 (ws). *Polygonum polygaloides* Meisn. subsp. *polygaloides* – Very common on basins and margins, especially in the east subregion, where growing in very dense, showy light-pink displays and sometimes producing a sweet fragrance, attracting abundant pollinators; C, E. **Rumex crispus* L. – Occasional on basins and margins; W, C, E. *Rumex maritimus* L. – Uncommon on basins of alkaline/salty pools; W, C, E. **Rumex patientia* L. – Rare on margins and basins; C. *Rumex salicifolius* Weinm. – Common, mostly on basins; W, C, E.

PORTULACACEAE. *Montia dichotoma* (Nutt.) Howell – Very common on margins; some populations in the central region grow across pool basins; C, E. *Montia linearis*

(Dougl. ex Hook.) E. Greene – Occasional on rocky margins; C, E. *Talinum spinescens* Torr. – Occasional on margins; some populations are flood-tolerant and grow across pool basins; W, C.

PRIMULACEAE. *Dodecatheon* sp. – Rare on margins; flood-intolerant; non-core; W.

RANUNCULACEAE. *Delphinium distichum* Geyer ex Hook. – Occasional or locally common on margins; W, C, E. *Myosurus apetalus* Gay var. *borealis* Whitem. – Occasional on margins; C. *Myosurus clavicaulis* M. Peck – Rare on basins; no intermediates with *M. minimus* found, though in California, this species is known to hybridize with its putative parent species, *M. minimus* and *M. sessilis* S. Watson; this appears to be a stable species in eastern Washington; W, C, E; 3210, 3215, 3315 (WTU). *Myosurus minimus* L. subsp. *minimus* – Very common on basins; W, C, E. *Ranunculus alismifolius* Geyer ex Benth. var. *alismifolius* – Found in a single pool, where dominant; E. *Ranunculus aquatilis* L. – Rare on basins of deep pools; W, C, E; 1277 (ws). *Ranunculus sceleratus* L. – Rare on basins of deep pools; C. **Ranunculus testiculatus* Crantz – Rare on margins; C.

ROSACEAE. *Amelanchier alnifolia* (Nutt.) Nutt. – Rare on margins; flood intolerant; non-core; W. *Geum triflorum* Pursh var. *triflorum* – Rare on margins, common in surrounding grasslands; flood intolerant; non-core; C. *Potentilla gracilis* Dougl. ex Hook. – Rare on margins, common in surrounding grasslands; flood-intolerant; non-core; W, C, E. *Potentilla rivalis* Nutt. – Occasional on basins of deep pools; C. *Rosa woodsii* Lindl. – Rare on margins, common in surrounding grasslands; probably flood-intolerant; non-core; C, E. *Sanguisorba occidentalis* Nutt. – Common on basins, occasional on margins; mostly germinating post-desiccation and overwintering as flooded rosettes to bloom the following summer; C, E.

RUBIACEAE. *Galium aparine* L. – Uncommon on margins, but very common on Mima mounds surrounding pools; flood-intolerant; non-core; W, C, E. *Galium trifidum* L. – Rare on basins; E.

SARCOBATACEAE. *Sarcobatus vermiculatus* (Hook.) Torr. – Rare on margins of alkaline/salty vernal pools; non-core; C, W.

SAXIFRAGACEAE. *Lithophragma glabrum* Nutt. – Rare on margins, but common on Mima mounds surrounding pools; flood-intolerant; non-core; C.

URTICACEAE. *Parietaria* cf. *hespera* B.D. Hinton – Uncommon on margins, but not highly flood-tolerant; occasional in surrounding grasslands; W, C, E; 3313 (WTU), 6216 (ws).

VALERIANACEAE. *Plectritis macrocera* Torr. & A. Gray – Occasional on margins; C.

VERBENACEAE. *Verbena bracteata* Lag. & Rodr. – Rare on margins or basins, germinating post-desiccation; flood-intolerant; non-core; C, W.